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A new species of *Leonhardia* Reitter, 1901 (Coleoptera, Leiodidae, Leptodirini) from Bosnia and Herzegovina, with a key to species of the genus

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Abstract

A new leptodirine leiodid beetle species belonging to the genus *Leonhardia* Reitter, 1901, *L. solaki* **sp. nov.**, from a pit in Bosnia and Herzegovina (western Balkan Peninsula) is described and diagnosed. Important morphological features of the new species are listed and photographed. The new species is endemic to the Dinarides of Bosnia and Herzegovina. A key for identification of species and subspecies of the genus *Leonhardia* is also provided.

Keywords

Balkan Peninsula, Dinarides, new species, round fungus beetles, troglobite

Introduction

The genus *Leonhardia* Reitter, 1901 (Coleoptera, Leiodidae, Leptodirini) contains the following six species: *Leonhardia delminiumica* Nonveiller, Pavićević, Rađa & Vujčić-Karlo, 2002 (from the Jama na Paklinama Pit and the Parampatuša Cave,

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Mt. Pakline, close to the town of Tomislavgrad); *L. droveniki* Perreau, 1999 (from the Kruščica Cave, Mt. Kruščica, close to the town of Vitez); *L. hilfi* Reitter, 1901 (from several pits on Mts. Vran and Čvrsnica, close to the town of Tomislavgrad); *L. jajcensis* S. Ćurčić & Rađa, 2014 (from the Kapnica Cave, Mt. Dnolučka Planina, close to the town of Jajce); *L. reitteri* Breit, 1902 (from several subterranean sites on Mts. Vlašić and Gola Planina, close to the towns of Travnik and Jajce, respectively); and *L. sebesicensis* S. Ćurčić, Pavićević & Mulaomerović, 2018 (from the Vilinska Pećina Cave, close to the town of Novi Travnik). It also includes the following five subspecies: *L. hilfi hilfi* Reitter, 1901 (from the Mijatova Jama Pit, Mt. Vran, close to the town of Tomislavgrad); *L. hilfi robusta* Knirsch, 1928 (from the Vuk Pit, Mt. Čvrsnica, close to the town of Tomislavgrad); *L. reitteri mersa* Knirsch, 1928 (from the Pećina pod Orlovcem Cave, Mt. Vlašić, close to the town of Travnik); *L. reitteri reitteri* Breit, 1902 (from several caves on Mt. Vlašić, viz., an unnamed ice cave, close to the town of Žepče; an unnamed ice cave, Harambašina Voda, close to the town of Travnik; an unnamed cave, Vruća Vrtača, close to the town of Travnik; Kapljica Cave, close to the town of Travnik; and an unnamed cave, Razvale, close to the town of Travnik); and *L. reitteri zariquieyi* Müller, 1937 (from several subterranean sites on Mt. Gola Planina, close to the town of Jajce, viz., Ćorića Jama Pit, Grič; Pećurina II Cave, Gornja Liskovica; and Zviječalka Cave, Barevo) (Fig. 1) (Reitter 1901, 1902; Breit 1902; Jeannel 1924; Knirsch 1928; Müller 1937; Perreau 1999, 2000; Nonveiller et al. 2002; Pretner 2011; Ćurčić et al. 2014, 2018). The genus is distributed in mountainous areas of central and southwestern Bosnia and Herzegovina, and species are both cave- and MSS-dwelling (sensu Giachino and Vailati 2010) (Perreau 2000, 2004, 2015; Ćurčić et al. 2014, 2018). They are spread from Mts. Dnolučka Planina, Vlašić, and Gola Planina in the north to Mts. Pakline and Vran in the south (Perreau 2000, 2004; Nonveiller et al. 2002; Ćurčić et al. 2014, 2018). Certain karstic areas in Bosnia and Herzegovina (especially in both the western part of the country and Herzegovina) are underinvestigated or even unexplored. For this reason, one may expect further findings of new leptodirine leiodid taxa in these regions in the future.

Two field trips in western Bosnia and Herzegovina conducted by the Špiljar Speleological Society (Split, Croatia) in June 2018 resulted in the discovery of a series of a new leiodid leptodirine species belonging to the genus *Leonhardia*, whose description and diagnosis are given in this study.

Materials and methods

Adult specimens of leiodid beetles were gathered by hand in a pit in the vicinity of the town of Glamoč (western Bosnia and Herzegovina). They were analysed in a laboratory of the Institute of Zoology, University of Belgrade - Faculty of Biology, Belgrade, Serbia. Both male and female genitalia were conserved on microscope slides in a medium consisting of Canada balsam and toluene. Beetles were glued on paper labels and studied as dry individuals. Taxonomically important morphological features were examined for

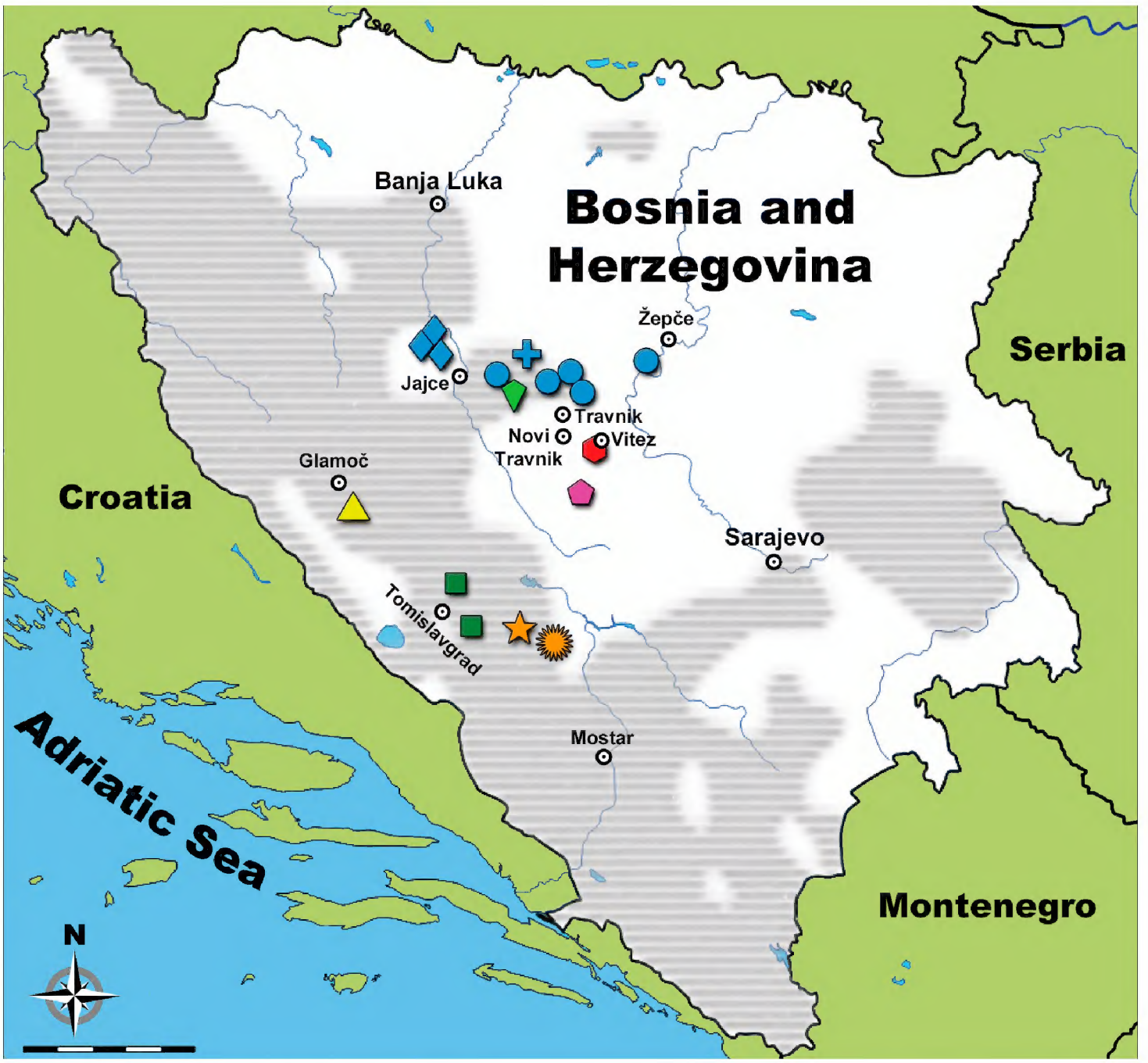

Figure 1. Map of Bosnia and Herzegovina showing locality records for all taxa of *Leonhardia*. The grey pattern indicates karst terrain *L. reitteri reitteri* (blue circles), *L. reitteri mersa* (blue cross), *L. reitteri zariquieyi* (blue rhombuses), *L. delminiumica* (green squares), *L. jajcensis* (lime deltoid), *L. hilfi hilfi* (orange star), *L. hilfi robusta* (orange sun), *L. sebesicensis* (pink pentagon), *L. droveniki* (red hexagon), *L. solaki* sp. nov. (yellow triangle). Scale bar: 50 km.

comparison. For that purpose, we used a Stemi 2000 binocular stereomicroscope (Carl Zeiss, Jena, Germany), a SMZ 18 binocular stereomicroscope (Nikon, Tokyo, Japan) with a DS-Fi1c digital camera (Nikon, Tokyo, Japan) attached, and an Axioskop 40 light microscope (Carl Zeiss, Jena, Germany). Beetles were additionally illuminated under binocular stereomicroscopes by an Intralux 5100 cold light source (Volpi, Schlieren, Switzerland). Detailed morphology of the new species was observed using a Tescan Mira 3 XMU field emission scanning electron microscope (FESEM) (Tescan, Brno, Czech Republic) at the Faculty of Technology and Metallurgy, University of Belgrade. Before analysis, the samples were coated with gold for 45 s using a Polaron SC502 Sputter Coater (Fisons, VG Microtech, East Sussex, England). The high-vacuum mode was used at an acceleration voltage of 10 kV. The index of electron beam intensity was 8.00. The electron beam current was 364 μA, while pressure in the column was around $1.3e^{-3}$ Pa.

Abbreviations of measurements

AL total antennal length including the scape;
A1L/A2L ratio of length of antennomere I to length of antennomere II;
A2L/A3L+A4L ratio of length of antennomere II to length of antennomeres III and IV combined;
A8L/A8W ratio of length of antennomere VIII to width of antennomere VIII;
A9L/A9W ratio of length of antennomere IX to width of antennomere IX;
A10L/A10W ratio of length of antennomere X to width of antennomere X;
A11L/A11W ratio of length of antennomere XI to width of antennomere XI;
EL/EW ratio of elytral length (as the linear distance measured along the suture from the elytral base to the apex) to maximum elytral width;
HL/HW ratio of head length to maximum head width;
M mean value for certain measurements;
PB/AM ratio of pronotal base length to anterior pronotal margin length;
PB/EB ratio of pronotal base length to elytral base length;
PL/PW ratio of pronotal length to maximum pronotal width (as the greatest transverse distance);
R range of total measurements performed;
TL total body length (measured from the anterior margin of the clypeus to the elytral apex).

Collections

CDP private collection of Dragan Pavićević, Belgrade, Serbia;
IZFB collection of the Institute of Zoology, University of Belgrade - Faculty of Biology, Belgrade, Serbia;
SSM collection of the Split Science Museum, Split, Croatia;

Other examined taxa

Leonhardia delminiumica Nonveiller, Pavićević, Rađa & Vujčić-Karlo, 2002: 13 topotype males and 16 topotype females, southwestern Bosnia and Herzegovina, Mt. Pakline, town of Tomislavgrad, village of Mandino Selo, Parampatuša Cave, 26.VII.2013, leg. T. Rađa (IZFB).

Leonhardia jajcensis S. Ćurčić & Rađa, 2014: holotype male, 21 paratype males and 39 paratype females, central Bosnia and Herzegovina, Mt. Dnolučka Planina, town of Jajce, village of Božikovac, Kapnica Cave, 5.V.2013 (pitfall trapping), leg. T. Rađa (IZFB); five paratype females, idem., 18.XI.2012, leg. T. Rađa (IZFB).

Leonhardia sebesicensis S. Ćurčić, Pavićević & Mulaomerović, 2018: holotype male and four paratype females, central Bosnia and Herzegovina, town of Novi Travnik, village of Sebešić, Vilinska Pećina Cave, 23.VIII.2014, leg. J. Mulaomerović (IZFB, CDP).

Results

Genus *Leonhardia* Reitter, 1901

***Leonhardia solaki* Ćurčić, Rađa, Vesović & Vrbica, sp. nov.**
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Figures 2, 3

Type material. ***Holotype:*** male (IZFB) labeled as follows: „WESTERN BOSNIA AND HERZEGOVINA: town of Glamoč, village of Skucani, Golubnjača kod Skucana Pit, 1,005 m a.s.l., 43°58'31.9"N, 16°54'43.6"E, June, 27, 2018, Tonći Rađa" (white label, printed)/„Holotypus *Leonhardia solaki* sp. nov. Ćurčić, Rađa, Vesović & Vrbica det. 2021" (red label, printed) (Fig. 2).

Paratypes (seven specimens). Same data as for holotype [two males and two females, IZFB, SSM]; same data as for holotype except for date [one male and two females, IZFB, June, 12, 2018]. All paratypes are labeled with white, printed locality labels and with red printed labels „Paratypus *Leonhardia solaki* sp. nov. Ćurčić, Rađa, Vesović & Vrbica det. 2021".

Etymology. The new species is named after Siniša Šolak, a geographer and naturalist, who was our guide during cave investigations conducted near the town of Glamoč.

Type locality. Western Bosnia and Herzegovina, town of Glamoč, village of Skucani, Golubnjača kod Skucana Pit.

Diagnosis. The new species is closely related to some other species of *Leonhardia* by its large size and by the presence of a high mesosternal carina. Those other species are *L. hilfi*, *L. reitteri*, *L. delminiumica*, *L. jajcensis*, and *L. sebesicensis* (Figs 1, 4) (Jeannel 1924; Nonveiller et al. 2002; Ćurčić et al. 2014, 2018).

Leonhardia solaki sp. nov. differs from *L. hilfi* in regard to AL in males (antennae exceeding the middle of elytra vs. antennae reaching the middle of elytra); A10L/A10W (less than 2.375 vs. more than 2.50); pronotum form (bell-shaped, lateral margins well-rounded anteriorly vs. subquadrate, lateral margins obtuse anteriorly); PL/PW (pronotum wider than long vs. pronotum as long as wide); shape of the mesosternal carina (higher, almost right-angled, posterior margin concave vs. lower, obtuse-angled, posterior margin somewhat elevated); shape of elytra (inversely ovate vs. widely oval); shape of the median lobe in dorsal view (apically flattened vs. apically narrowed); length of the median lobe (barely longer than parameres vs. markedly longer than parameres); shape and size of the basal bulb in dorsal view (larger, rounded vs. smaller, not rounded); and shape of the aedeagus in lateral view (median lobe more curved, basal bulb larger vs. median lobe less curved, basal bulb smaller) (Figs 2–4) (Reitter 1901; Jeannel 1924; Knirsch 1928; Perreau 1999; Nonveiller et al. 2002).

Leonhardia solaki sp. nov. is easily distinguished from *L. reitteri*, from which it differs with respect to AL (antennae exceeding the middle of elytra in males and reaching the middle of elytra in females vs. antennae barely reaching the middle of body); A2L/A3L+A4L (antennomere II shorter than the following two antennomeres combined vs.

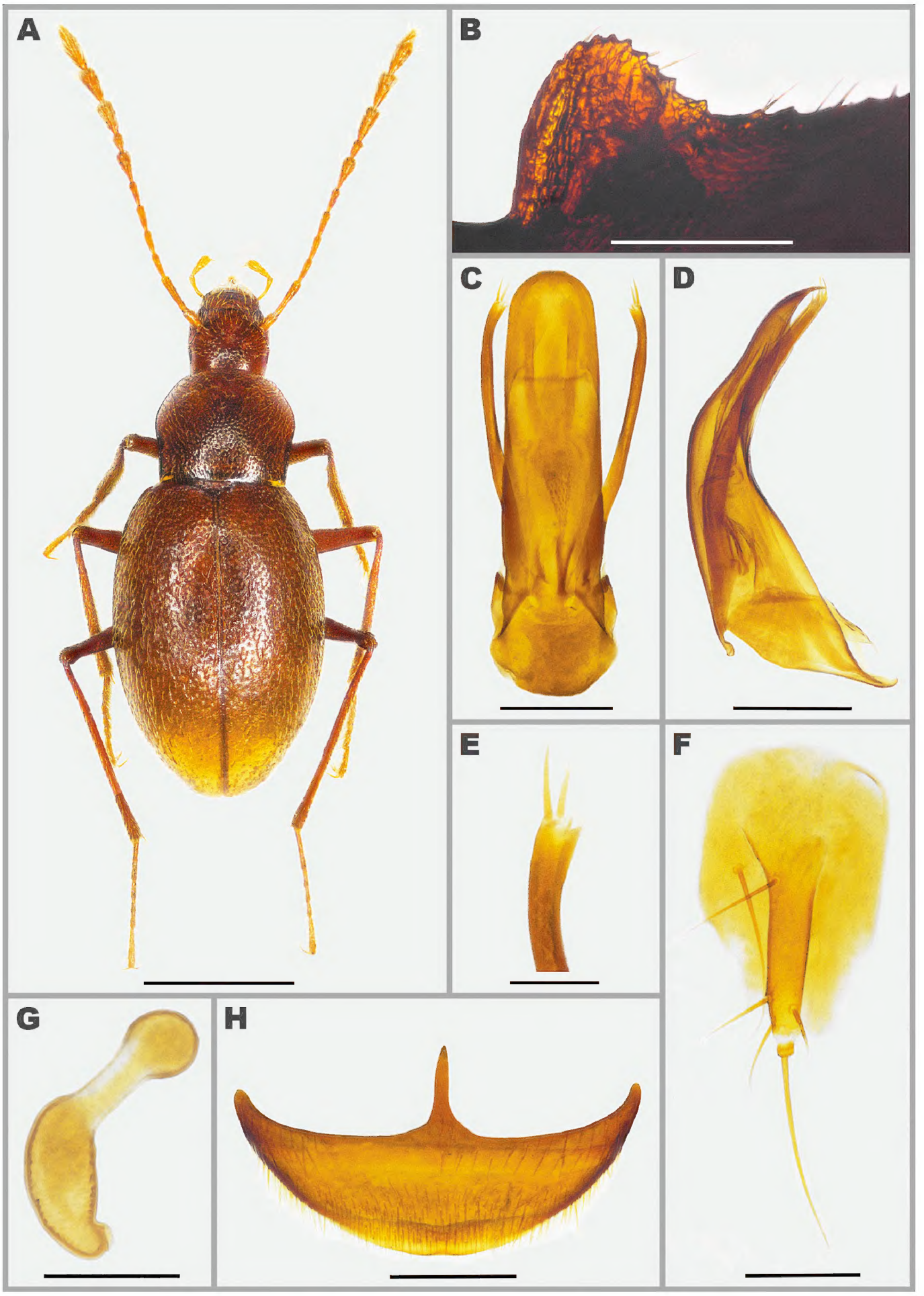

Figure 2. Bright-field images of morphological features of *Leonhardia solaki* sp. nov. from the Golubnjača kod Skucana Pit, village of Skucani, close to the town of Glamoč, western Bosnia and Herzegovina **A** holotype male, habitus, dorsal aspect **B** holotype male, mesosternal carina, lateral aspect **C** holotype male, aedeagus, dorsal aspect **D** holotype male, aedeagus, lateral aspect **E** holotype male, left paramere apex, dorsal aspect **F** paratype female, left gonostylus, dorsal aspect **G** paratype female, spermatheca, lateral aspect **H** paratype female, abdominal segment VIII, ventral aspect. Scale bars: 1.0 mm (**A**); 0.2 mm (**B–D, H**); 0.1 mm (**F, G**); 0.05 mm (**E**).

antennomere II as long as the following two antennomeres combined); A8L/A8W (M in males 2.06, in females 1.58 vs. 1.50 in both genders); A10L/A10W (R in females 1.54–1.78 vs. more than 2.00 in both genders); shape of the hind pronotal angles (obtuse vs. right or weakly acute); shape of the mesosternal carina (almost right-angled, anterior margin convex, posterior margin regularly concave vs. obtuse-angled, anterior margin obtuse, posterior margin deeply incised); shape of elytra (inversely ovate vs. oval); shape of the median lobe in dorsal (wider in apical half, apically flattened vs. thinner in apical half, apically narrowed) and lateral (more elongate vs. less elongate) views; length of the median lobe (barely longer than parameres vs. markedly longer than parameres); and position of parameral setae in dorsal view (inner pre-apical seta somewhat separated from two remaining setae vs. all setae equidistant) (Figs 2–4) (Breit 1902; Jeannel 1924; Knirsch 1928; Müller 1937; Perreau 1999; Nonveiller et al. 2002).

Leonhardia solaki sp. nov. differs from *L. delminiumica* in regard to TL (R 3.40–3.65 mm in males, 3.55–3.93 mm in females vs. R 3.10–3.20 mm in males, 3.40 mm in a female); A8L/A8W (M 2.06 in males, 1.58 in females vs. antennomere VIII barely longer than broad); shape of the mesosternal carina (almost right-angled, posterior margin less concave vs. obtuse-angled, posterior margin more concave); shape of the median lobe in dorsal (apically flattened, with a rounded apex vs. apically narrowed, with a pointed apex) and lateral (more curved, wider vs. less curved, narrower) views; length of the median lobe (barely longer than parameres vs. markedly longer than parameres); size of the basal bulb in dorsal view (larger vs. smaller); and position of parameral setae in dorsal view (inner pre-apical seta closer to the two remaining setae vs. inner pre-apical seta farther away from the two remaining setae) (Figs 2–4) (Nonveiller et al. 2002).

Leonhardia solaki sp. nov. is easily distinguished from *L. jajcensis*, from which it differs with respect to AL in females (antennae reaching the middle of elytra vs. antennae ending before the middle of elytra); shape of the hind pronotal angles (obtuse vs. almost right); shape of the mesosternal carina (higher, anterior margin more convex, posterior margin more concave vs. lower, anterior margin less convex, posterior margin less concave); form of the elytra (more elongate vs. less elongate); shape of the median lobe in dorsal (apically flattened vs. apically narrowed) and lateral (more thickened in its basal half, less convex ventrally vs. less thickened in its basal half, more convex ventrally) views; length of the median lobe (barely longer than parameres vs. markedly longer than parameres); size of the basal bulb in dorsal view (larger vs. smaller); and position of parameral setae in dorsal view (inner pre-apical seta farther away from the two remaining setae vs. inner pre-apical seta closer to the two remaining setae) (Figs 2–4) (Ćurčić et al. 2014).

Leonhardia solaki sp. nov. differs from *L. sebesicensis* in regard to AL in females (antennae reaching the middle of elytra vs. antennae ending before the middle of elytra); shape of the hind pronotal angles (obtuse-angled in both genders vs. almost right-angled in males); shape of the pronotum and elytra (less elongate vs. more elongate); shape of the mesosternal carina (apically rounded vs. apically toothed); shape of the median lobe in dorsal (apically flattened vs. apically rounded) and lateral (more curved, narrower in apical half vs. less curved, wider in apical half) views; length of the median

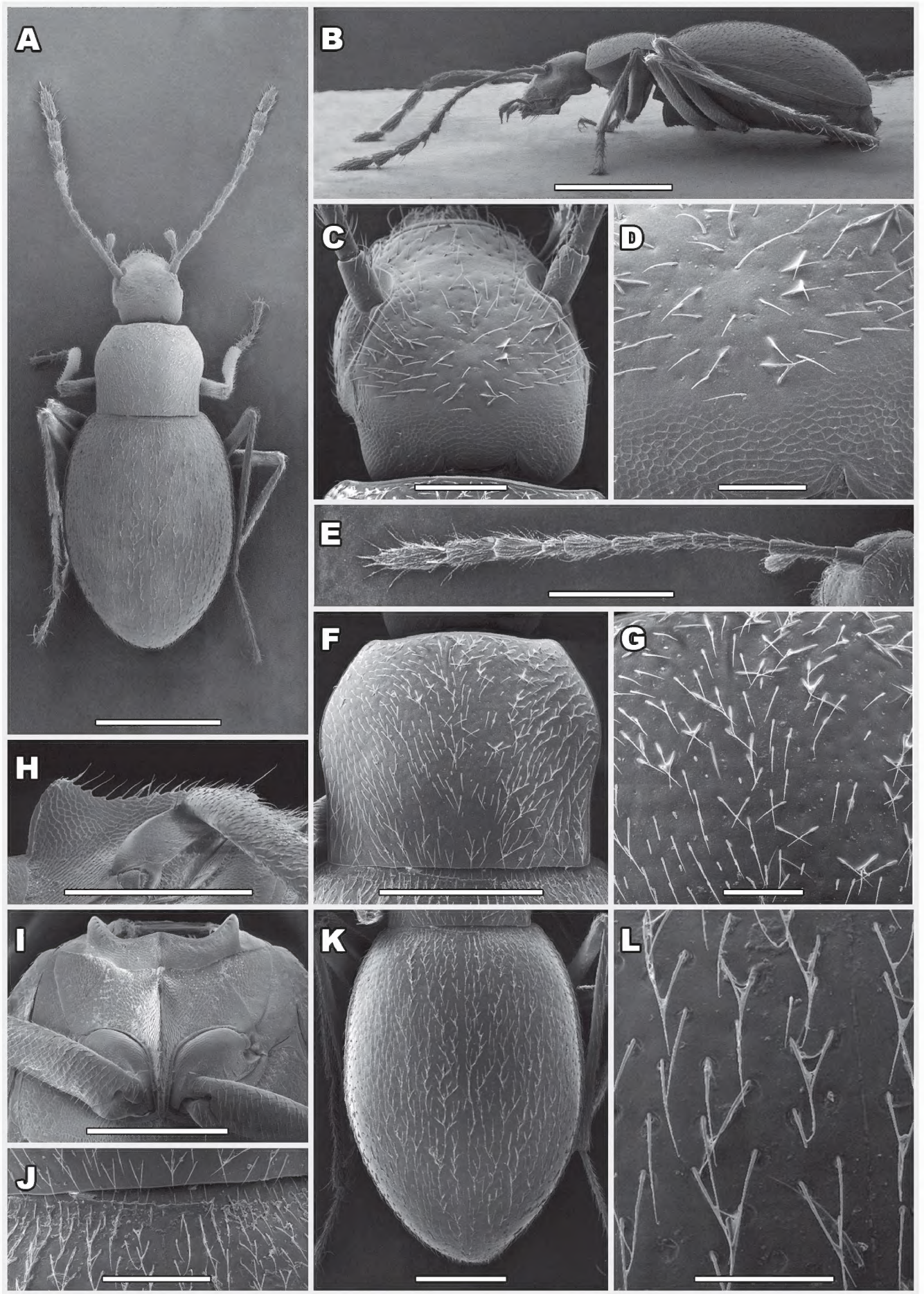

Figure 3. SEM images of morphological features of *Leonhardia solaki* sp. nov. from the Golubnjača kod Skucana Pit, village of Skucani, close to the town of Glamoč, western Bosnia and Herzegovina **A** paratype male, habitus, dorsal aspect **B** paratype male, habitus, lateral aspect **C** paratype male, head, dorsal aspect **D** paratype male, microsculpture of head, dorsal aspect **E** paratype male, right antenna, dorsal aspect **F** paratype male, pronotum, dorsal aspect **G** paratype male, microsculpture of pronotum, dorsal aspect **H** paratype male, mesosternal carina, lateral aspect **I** paratype male, mesoventrite, ventral aspect **J** paratype male, scutellum, dorsal aspect **K** paratype male, elytra, dorsal aspect **L** paratype male, microsculpture of elytra, dorsal aspect. Scale bars: 1.0 mm (**A, B**); 0.5 mm (**E, F, H, I, K**); 0.2 mm (**C, J**); 0.1 mm (**D, G, L**).

lobe (barely longer than parameres vs. markedly longer than parameres); and position of parameral setae in dorsal view (inner pre-apical seta somewhat separated from two remaining setae vs. all setae equidistant) (Figs 2–4) (Ćurčić et al. 2018).

Description. Medium-sized leptodirine. TL M 3.62 mm (3.55 mm in males, 3.69 mm in females), R 3.40–3.93 mm (3.40–3.65 mm in males, 3.55–3.93 mm in females).

Habitus: Body shape pholeuonoid, colour reddish-brown (Figs 2A, 3A, B).

Integument: Shiny, microsculptured (Fig. 3D, G, L). Body covered with a number of densely distributed deep punctures and yellow pubescence of medium length (erect on head, recumbent on both pronotum and elytra).

Head: Longer than wide (HL/HW M 1.11, R 1.06–1.19), anophthalmous, with no occipital carina (Figs 2A, 3C). Labrum slightly emarginate, with several long setae. Penultimate maxillary palpomere widened apically. Ultimate maxillary palpomere short, thin, gradually narrowing apically. Vertex with a longitudinal impression. Antennae inserted in middle third of head, slender, narrow proximally, slightly dilated distally, longer in males, AL M 2.15 mm, R 1.93–2.33 mm (2.165–2.33 mm in males, 1.93–2.165 mm in females), exceeding middle of elytra in males and reaching middle of elytra in females (Figs 2A, 3E). Antennomere I short and wide. A1L/A2L M 0.54, R 0.52–0.58. Antennomere II narrow, elongate, shorter than III and IV combined (A2L/A3+A4L M 0.86, R 0.79–0.90). Antennomeres III–VI of similar shape and size, narrow, among which V is the longest. Antennomeres VII and IX–XI widened (VII, IX, and X dilated distally), large, among which VII is the shortest in males, VIII the shortest in females, and XI the longest in both sexes. Antennomere VIII small, elongate in males (A8L/A8W M 2.06, R 1.82–2.40), wide in females (A8L/A8W M 1.58, R 1.33–1.90). A9L/A9W in males M 2.35 (R 2.25–2.50), in females M 1.68 (R 1.60–1.78). A10L/A10W in males M 2.27 (R 2.21–2.375), in females M 1.65 (R 1.54–1.78). Ultimate antennomere slender, narrowing apically, A11L/A11W in males M 3.10 (R 2.54–3.50), in females M 2.82 (R 2.67–3.00).

Prothorax: Pronotum bell-shaped, transverse (PL/PW M 0.87, R 0.84–0.91), widest slightly after anterior third, markedly broader than head (Figs 2A, 3F). Lateral margins well-rounded anteriorly, somewhat concave posteriorly, sub-parallel basally. Pronotal base straight, markedly shorter than elytral base (PB/EB M 0.95, R 0.90–0.99). PB/AM M 1.40, R 1.18–1.55. Anterior margin somewhat convex medially. Fore pronotal angles small, rounded, obtuse. Hind pronotal angles obtuse, prominent, not protruding backwards. Pronotal disc moderately convex (Fig. 3B).

Mesothorax: Mesosternal carina high anteriorly, low posteriorly (Figs 2B, 3H). Anterior margin convex, posterior margin concave, with a few setae. Tooth obtuse, rounded. No mesoventral processus on mesoventrite (Fig. 3I). Scutellum large, triangular (Figs 2A, 3J).

Metathorax: Metasternum without carina.

Elytra: Wide, obovoid, slightly wider in females (EL/EW in males M 1.47, R 1.40–1.57; in females M 1.44, R 1.41–1.48), markedly wider than pronotum (Figs 2A, 3K). Maximum width slightly before middle. Lateral margins arcuate. Marginal furrows visible on nearly entire elytra. Shoulders weakly expressed, almost rounded. Elytral disc markedly convex, gently declining basally and steeply declining apically in lateral

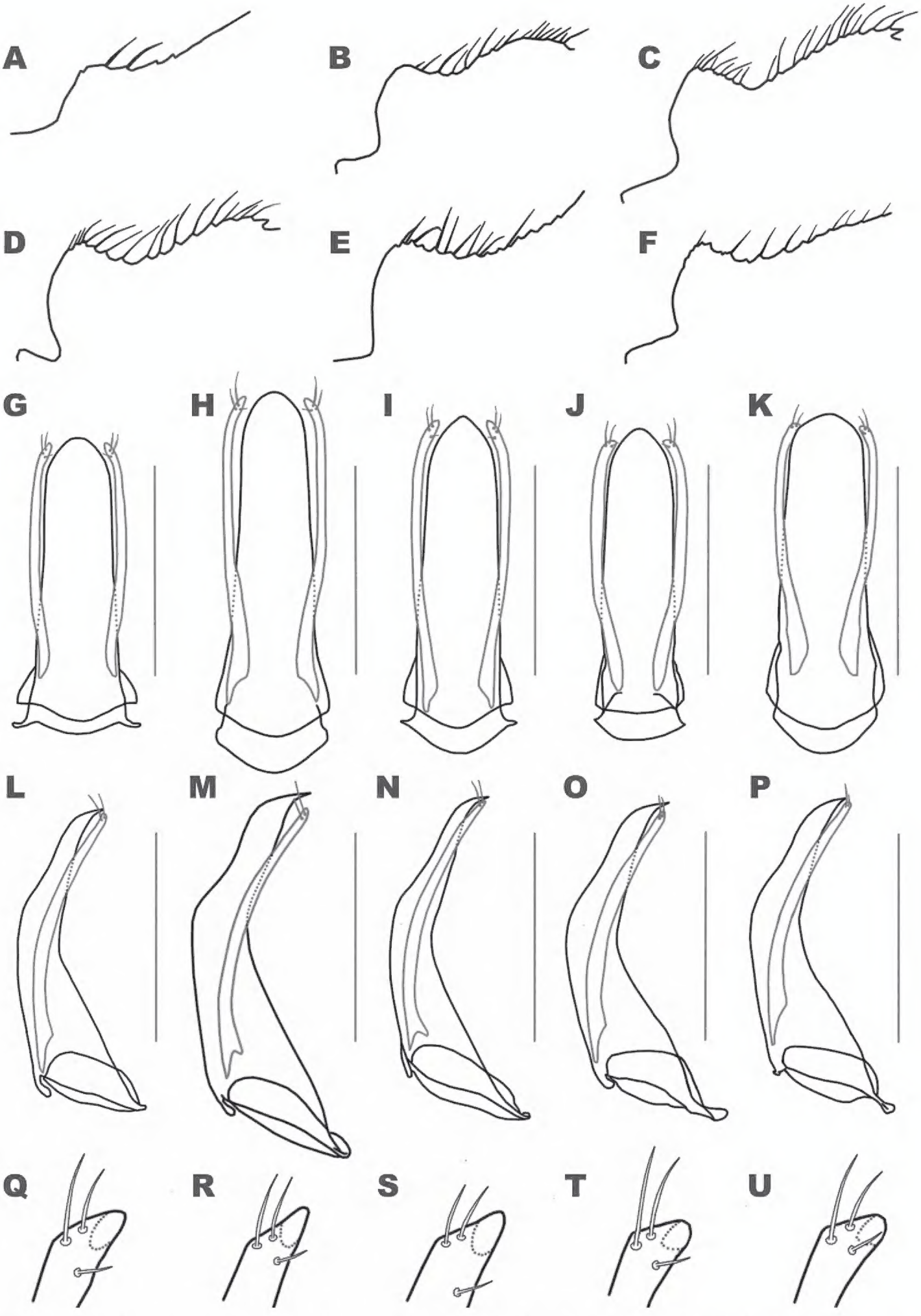

Figure 4. Different morphological features of *Leonhardia* [*L. droveniki* (**A**) *L. hilfi* (**B, G, L, Q**) *L. reitteri* (**C, H, M, R**) *L. delminiumica* (**D, I, N, S**) *L. jajcensis* (**E, J, O, T**) and *L. sebesicensis* (**F, K, P, U**)] [modified after Nonveiller et al. (2002) and Ćurčić et al. (2014, 2018)] **A–F** mesosternal carina, lateral aspect **G–K** aedeagus, dorsal aspect **L–P** aedeagus, lateral aspect **Q–U** left paramere apex, dorsal aspect. Scale bars: 0.5 mm (**G–P**).

view (Fig. 3B). Sutural striae developed. Elytral apex attenuated, rounded. Pygidium covered by elytra.

Legs: Elongate (Fig. 2A). Femora widened basally, constricted sub-apically. Tibiae thin, very gently curved, gradually widening distally, each with several spines. Each fore tibia with an outer distal brush-like structure. Male fore tarsi five-segmented, weakly dilated. Tarsal claws elongate, narrow, curved, pointed apically.

Male genitalia: Aedeagus elongate, straight, thin, sclerotized (Figs 2C, D). Basal bulb small and rounded in dorsal view (Fig. 2C), moderately large in lateral view (Fig. 2D). Median lobe in dorsal view sub-parallel, rounded anteriorly, with a flattened apex, longer than parameres (Fig. 2C). Median lobe in lateral view curved, straight in basal half, sub-apically concave dorsally, almost straight ventrally in basal part, with an acute apex curved downwards (Fig. 2D). Parameres slender, narrow, arcuate, sub-apically curved towards exterior, each with a dilated rounded apex in dorsal view (Figs 2C, E), while gently narrowing distally in lateral view (Fig. 2D). Paramere bearing three setae: two strong, long, in apical and pre-apical position, respectively, and one inner, thin, short, in pre-apical position (Fig. 2E). Two long parameral setae close-set, short one somewhat separated, positioned somewhat below level of other two parameral setae (Fig. 2E). Endophallus elongate, tubular. Copulatory piece having a Y-shaped phanera and two lateral basal sclerifications, in front of which a weakly chitinized structure resembling teeth is present. In addition, two lateral bands are present in apical half of median lobe (Fig. 2C).

Female genitalia: Gonostyli slender, thin, gradually narrowing distally, straight, pointed apically (Fig. 2F). Each gonostylus carrying one apical seta, three inner setae, and one outer seta (Fig. 2F). Spermatheca elongate, chitinized, curved, constricted posteriorly in sub-apical part, spherical apically (Fig. 2G).

Female abdominal sternite VIII: Large, transverse, with a thin anterior process, carrying pubescence (Fig. 2H).

Intraspecific variability. A certain level of intraspecific variability is observed in the new species. Several morphological differences between males and females point to the occurrence of sexual dimorphism. To be specific: (i) males are on average slightly shorter than females; (ii) the antennae in males are longer than in females; (iii) antennomeres VIII–XI in males are more slender than in females; (iv) the head in males is larger than in females; (v) the pronotum in males is more elongate than in females; (vi) the elytra in males are more elongate than in females.

Geographic distribution. Thus far, the species is known only from its type locality – the Golubnjača kod Skucana Pit, situated in the village of Skucani, close to the town of Glamoč in western Bosnia and Herzegovina. This site represents the westernmost location of a *Leonhardia* species. We assume that the new species probably inhabits other subterranean sites in the surrounding areas of western Bosnia and Herzegovina, although one of us (TR) visited the Ledenjača Cave situated in the same village (Skucani), but found no specimens of the new species there.

Bionomy and habitat. All specimens of *L. solaki* sp. nov. were collected deep in the Golubnjača kod Skucana Pit. They were recorded at this subterranean site at

a depth of 30 m under conditions of permanent darkness and high humidity, along with the presence of trickling water. All individuals of *L. solaki* sp. nov. were gathered manually from the floor and walls in the innermost part of the pit. Aside from the new species, Golubnjača kod Skucana Pit is inhabited by another subterranean leiodid, *Parapropus ganglbaueri obenbergeri* Mařan, 1943, which is recorded in the same habitat where individuals of the new species were found, so these two taxa can be treated as sympatric. The same pit is also the type locality of the recently described moth fly *Psychoda glamocensis* Wagner & Rada, 2020 (Wagner and Rada 2020).

Key for identification of species and subspecies of *Leonhardia* (Figs 2–4)

1 Smaller body size (2.80–3.00 mm in length). Mesosternal carina low (Fig. 4A) .. .. ***L. droveniki* Perreau, 1999**

– Larger body size (3.10–4.00 mm in length). Mesosternal carina high (Figs 2B, 3H, 4B–F) **2**

2 Anterior margin of mesosternal carina obtuse, posterior margin deeply incised (Fig. 4C). Median lobe in lateral view less elongate and more curved (Fig. 4M) (*L. reitteri* Breit, 1902) **3**

– Anterior margin of mesosternal carina convex, posterior margin regularly concave (Figs 4B, D–F). Median lobe in lateral view more elongate and less curved (Figs 4L, N–P) **5**

3 Larger body size (3.50–3.70 mm in length). Pronotum less transverse. Lateral elytral margins more arcuate, elytra apically rounded **4**

– Smaller body size (3.20 mm in length). Pronotum more transverse. Lateral elytral margins less arcuate, elytra apically pointed ..... ***L. reitteri mersa* Knirsch, 1928**

4 Pronotum narrowed basally, elytra narrower and less convex, pronotal depressions lacking or barely discernible ..... ***L. reitteri reitteri* Breit, 1902**

– Pronotum not narrowed basally, elytra wider and more convex, two depressions present on pronotum ..... ***L. reitteri zariquieyi* Müller, 1937**

5 Mesosternal carina almost right-angled (Figs 2A, 3H, 4E) **6**

– Mesosternal carina obtuse-angled (Figs 4B, D, F) 7

6 Hind pronotal angles almost right. Mesosternal carina lower, anterior margin less convex, posterior margin less concave (Fig. 4E). Median lobe in dorsal view apically narrowed, markedly longer than parameres (Fig. 4J) .... ***L. jajcensis* S. Ćurčić & Rađa, 2014**

– Hind pronotal angles obtuse (Figs 2A, 3F). Mesosternal carina higher, anterior margin more convex, posterior margin more concave (Figs 2B, 3H). Median lobe in dorsal view apically flattened, barely longer than parameres (Fig. 2C) .... ***L. solaki* sp. nov.**

7 Median lobe in dorsal view apically pointed (Fig. 4I). Inner pre-apical seta markedly separated from two remaining parameral setae (Fig. 4S) .... ***L. delminiumica* Nonveiller, Pavićević, Rađa & Vujčić-Karlo, 2002**

– Median lobe in dorsal view apically rounded (Figs 4G, K). Parameral setae close-set (Figs 4Q, U) **8**

8 Mesosternal carina higher, apically toothed (Fig. 4F). Median lobe in dorsal view wider, apically rounded (Fig. 4K). Parameral setae equidistant (Fig. 4U) .... ***L. sebesicensis* S. Ćurčić, Pavićević & Mulaomerović, 2018**

– Mesosternal carina lower, apically rounded (Fig. 4B). Median lobe in dorsal view narrower, apically flattened (Fig. 4G). Inner pre-apical parameral seta somewhat separated from two remaining parameral setae (Fig. 4Q) (*L. hilfi* Reitter, 1901) ... **9**

9 Smaller body size (3.40–3.50 mm in length). Antennae shorter and narrower. Punctures smaller. Pubescence shorter ..... ***L. hilfi hilfi* Reitter, 1901**

– Larger body size (3.80–4.00 mm in length). Antennae longer and wider. Punctures larger. Pubescence longer ..... ***L. hilfi robusta* Knirsch, 1928**

Discussion

In the chapter on the family Leiodidae of the recent Catalogue of Palaearctic Coleoptera, Perreau (2015) mentioned *L. delminiumica* as an endemic of Mt. Pakljina Planina, but in fact the correct name of the mountain is Mt. Pakline. Furthermore, Perreau (2000, 2015) reported that *L. droveniki* inhabits Ilidža (without any additional data, this location refers to a municipality of the city of Sarajevo), but the given species lives in a cave on Mt. Kruščica, in the environs of the town of Vitez. Knirsch (1928) erroneously indicated several type localities of certain *Leonhardia* species collected by the speleologist Leo Weirather (Innsbruck, Austria). Weirather relied on the sale of beetle specimens to fund his research and tried to protect his discoveries from competition by hiding his collecting locations under assumed names and code numbers. Weirather's diaries were recently published by Giachino and Lana (2005) and Hauser (2011). Subsequently, Pretner (2011) decoded a list of caves and above-ground collecting sites visited by Weirather. As for Weirather's material of *Leonhardia*, the type locality of *L. hilfi robusta* is the Vuk Pit situated on Vilinac in the northern part of Mt. Čvrsnica [not soil from the Strmenica site on Mt. Plasa, as first stated by Knirsch (1928) and later followed by Perreau (2000, 2015) and Ćurčić et al. (2014)], a situation that was later clarified by Pretner (2011). Additionally, Knirsch (1928) stated that the type locality of *L. reitteri mersa* is Vrbanje in the environs of Banja Luka (in fact the settlement of Vrbanja is located within the city limits of Banja Luka). As was later indicated by Müller (1937) and Pretner (2011), the correct name of this type locality is the Pećina pod Orlovcem Cave in the village of Koričani on the northern slope of Mt. Vlašić. Perreau (2000) and Ćurčić et al. (2014) indicated that an unnamed ice cave at the Harambašina Voda site on Mt. Vlašić is the type locality of *L. reitteri reitteri* (in fact this site is the type locality of *L. reitteri retusa* Knirsch, 1924, a synonym of *L. reitteri reitteri*). However, this location [initially mentioned by Breit (1902) as an unnamed cave from the northern mountains of Bosnia] should correctly be referred to as an unnamed ice cave south of the town of Žepče, as was first stated by Reitter (1902) and later confirmed by Jeannel (1924) and Pretner (2011).

Jeannel (1910) placed the genus *Leonhardia* in the "*Apholeuonus*" phyletic series, which was later followed by Jeannel (1924) and Perreau (2000). This series is characterized by the great variety of genera belonging to the group, with form of the body

varying from globular and vesicular to narrow and elongate (Jeannel 1924). The body pubescence is scattered, erect, and short, each hair placed at the bottom of a large puncture. Combs on the fore tibias are reduced and the femora are narrowed in the apical third in most cases. Armature of the endophallus includes one ventral Y-shaped piece, two dorsal parts, and two lateral parts. Dorsal parts of the armature of the endophallus are fused along the median line and constitute a tooth that is apically pointed in the genera *Leonhardia*, *Adelopidius* Apfelbeck, 1907, and *Apholeuonus* Reitter, 1889, suggesting that the mentioned genera are closely related (Jeannel 1924).

The leiodid tribe Leptodirini is one of the largest and most diverse groups of subterranean insects (Ribera et al. 2010). Their distribution is restricted to the Palaearctic region, with the variety of forms being highest in the Mediterranean (Perreau 2000, 2005). Both morphological and molecular studies have been applied in order to determine phylogeny of the tribe (Perreau and Pavićević 2008b; Ribera et al. 2010; Fresneda et al. 2011; Njunjić et al. 2017, 2018; Antunes-Carvalho et al. 2019; Perreau 2019). Molecular phylogenetic studies treating the western Mediterranean (both Sardinian and Pyrenean) Leptodirini were initially conducted on the Sardinian taxa (Sbordoni 1980; Caccone and Sbordoni 2001). They were followed by analysis of the Pyrenean fauna (Ribera et al. 2010), which indicated that the principal Pyrenean subterranean lineages were split out prior to the Early Oligocene (Ribera et al. 2010). With 36 genera and 103 species inhabiting subterranean habitats, Leptodirina is one of the most diverse subtribes of the tribe Leptodirini (Njunjić et al. 2017). In regard to Dinaric representatives of the subtribe Leptodirina, studies devoted to the phylogeny of individual taxa or the entire group are very few, being either morphology-based (Perreau and Pavićević 2008a) or molecular-based (Njunjić et al. 2017, 2018). Perreau and Pavićević (2008b) stated that the monophyly of Leptodirina is very questionable because a number of taxa are highly troglobiomorphic and because numerous morphological features are potentially homoplasic. Njunjić et al. (2018) maintained that the subtribe is in fact polyphyletic inasmuch as three genera of Leptodirina (*Charonites* Apfelbeck, 1907, *Apholeuonus*, and *Parapropus* Ganglbauer, 1899) constitute a well-supported clade, which represents a sister clade in relation to other Leptodirini, while two genera of the same subtribe (*Remyella* Jeannel, 1931 and *Rozajella* S. Ćurčić, Brajković & B. Ćurčić, 2007) form a clade with Bathysciina+Bathysciotina, which is weakly supported in both molecular and morphological terms (Njunjić et al. 2018). It was estimated that the latter clade was formed about 32 million years ago, during the Early Oligocene, while the one which includes the genera *Charonites*, *Apholeuonus*, and *Parapropus* originated more recently (about 25 million years ago), during the Late Oligocene (Njunjić et al. 2018). According to this and on the basis of morphological similarities between those three genera and *Leonhardia*, we suggest that the latter genus originated during the Late Oligocene too. The subtribal assignation of *Remyella*, *Rozajella* and *Nonveilleriella* Perreau & Pavićević, 2008 is questionable and should be reassessed (Njunjić et al. 2017, 2018). To clarify the phylogenetic status of the subtribe Leptodirina as a whole and of its genera, it is essential to study as many genera as possible in this manner.

The differentiation of *L. solaki* sp. nov. and other species of *Leonhardia* in a limited part of the Balkan Peninsula was brought about by the Alpine Orogeny, successive evolution of the subterranean karstic relief in the Cenozoic, and specific palaeoclimatic events in the Neogene. These processes enabled the creation of a number of new epigean and hypogean habitats suitable for conservation of the old native Aegean fauna (Ćurčić et al. 2015). Finding of the new hypogean leiodid species described and diagnosed herein calls attention to the fact that the Dinarides represent a remarkable hotspot of subterranean biodiversity. Multiple colonization of subterranean niches of the Dinarides by different lineages of beetles in different chronological phases during the Tertiary was possible (Casale et al. 2004). It is apparent that the great number of endemics occurring in the Dinarides is related to the fragmentation of hypogean environments, which promoted the evolutionary drift in isolated populations allowed by the long-term persistence and higher stability of subterranean habitats compared to epigean ones (Gibert and Deharveng 2002). During cool and dry phases of the Pleistocene, subterranean sites (caves, pits, and the fissure network in bedrock) on the Balkan Peninsula might have become fewer and separated from each other, thereby enabling allopatric speciation of subterranean leptodirine leiodid beetles influenced by vicariant range fragmentation (Polak et al. 2016).

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